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Chapter V

Vascular plant litter input in subarctic peat bogs changes soil invertebrate diets and decomposition patterns

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Abstract

In high-latitude ecosystems climate change induced plant community shifts towards dominance of shrubs and trees will potentially have large consequences for soil carbon dynamics. Changes in the litter layer due to an altered quantity and quality of litter input, or by its indirect effect on microclimatic conditions, might affect the decomposer community.

To be able to predict the effects of increased litter input on decomposers and consequently on soil carbon dynamics, we studied the contribution of soil invertebrates (springtails) to carbon processing in a high-latitude peat bog system. Moreover, we assessed the effects of changing litter inputs on their abundance, diversity and diet choice, using a ^{13}C tracer approach.

The $\delta^{13}C$ signatures of springtails showed that they contributed significantly to the decomposition of peat moss (*Sphagnum fuscum*) and that species feed on different carbon sources. However, when vascular plant litter (*Betula pubescens*) entered the *Sphagnum* peat ecosystem, the $\delta^{13}C$ signatures of the springtails, and thus their role in organic matter processing changed and species-specific differences on decomposition disappeared. There were only slight changes in springtail species composition and abundances in *Sphagnum-Betula* mixtures, but more importantly all springtail species showed a strong dietary preference for *Betula*; 67% of their diet contained carbon originating from *Betula* litter. Decomposition patterns corresponded to these findings; mass loss (after 406 days of incubation) of *Betula* increased from 16.1% to 26.2% when decomposing in combination with *Sphagnum*, and *Sphagnum* decomposed even slower in combination with *Betula* litter (from 4.7% to 1.9%).

Our results indicate that the change in litter chemistry is the main way in which vascular litter inputs alter the role of high-latitude soil invertebrates in carbon turnover. Soil invertebrates are plastic in their diet choice, which implies that changes in carbon turnover rates in situations where vegetation shifts occur, might well be due to diet shifts of the present decomposer community rather than by changes in species composition.

Introduction

Understanding and predicting effects of climate change on ecosystem processes is an urgent challenge for ecologists. One major difficulty of this herculean task is that climate change does not only influence ecosystem processes directly through temperature rise and changed precipitation regimes, but also indirectly by effects on plant and animal communities (Wookey *et al.* 2009; Kardol *et al.* 2010). These latter effects are especially apparent in high latitude and temperate alpine ecosystems, where shifts towards dominance of shrubs and trees over existing moss communities due to climate change have been predicted and observed (Sturm *et al.* 2001; Chapin *et al.* 2005; Elmendorf *et al.* 2012a; Elmendorf *et al.* 2012b). Through subsequent ecosystem feedbacks and cascade processes (Wookey *et al.* 2009), changes in vegetation composition can alter patterns of growth, allocation and nutrient uptake by the vegetation. In turn this will affect dead organic matter quantity and quality and, thereby, the soil decomposer community and decomposition rates (Gogo *et al.* 2011). Soil invertebrates, a key group of litter decomposers and microbivores in these ecosystems, are expected to respond strongly to changes in plant dominance (Bardgett and Wardle 2010), which might have large consequences for organic matter breakdown (Laiho *et al.* 2001) and, thereby, soil carbon dynamics.

One important pathway by which altered plant cover and composition cascade down to the soil invertebrate community is by litter input to the soil ecosystem (Bardgett and Wardle 2010). Increases in 'shrubbiness' (Wookey *et al.* 2009) of moss dominated high latitude ecosystems will alter the quality and quantity of litter input (Cornelissen *et al.* 2007), which might, subsequently, change the soil invertebrate community composition and the spatial patterning of component species (Hättenschwiler *et al.* 2005; Berg 2012). Chemical properties of litter directly affect the soil invertebrate community mainly by determining their food quality, or indirectly through the composition and quality of the fungi, an important food source for microbivores (Hogervorst *et al.* 2003). Since soil invertebrate species select food sources of higher quality if they can (Ponge 2000; Schneider and Maraun 2005), input of litter with higher quality could lead to changes in spatial patterning of soil invertebrate species density and composition, both horizontally and vertically (Berg and Bengtsson 2007). This, in turn, may feed back on the breakdown of this litter.

Additionally, a change in the physical properties of litter might structure soil invertebrate communities by altering the local microclimatic conditions (Coulson *et al.* 1993; Hättenschwiler *et al.* 2005) to which soil invertebrates are very sensitive (Huhta and Hanninen 2001). Changes in these conditions over space and/or time lead to spatial patterning of soil invertebrates (Faber and Joosse 1993; Berg *et al.* 1998; Briones *et al.* 2007) and shifts in species composition (Makkonen *et al.* 2011). Knowledge about the importance of variation in the physical aspects of litter relative to chemical quality is important for understanding and predicting its effects on the decomposer community, since species differ in their sensitivities to alterations in microclimate versus litter chemistry (Krab *et al.* 2010).

The consequences of shifts in the soil invertebrate community structure might affect decomposition rates, since soil invertebrates are functionally dissimilar in their preferences and activities with respect to consumption of both litter and litter-dwelling microbes (Faber and Verhoef 1991; Setälä *et al.* 1998; Heemsbergen *et al.* 2004; Vos *et al.* 2011). Spatially, invertebrates have specific effects on the decomposition process of different litter species (horizontal patterning) and in subsequent strata of a given litter species (vertical patterning). In shallow fresh litter layers of temperate pine forests, for instance, the activities of soil invertebrates are known to immobilize nutrients, whereas in older fragmented litter of the same species, deeper in the soil profile, nutrients are mobilized by their feeding activities (Faber 1991). Shifts in spatial patterning or in species composition, therefore might have direct consequences for organic matter breakdown and related carbon fluxes (Briones *et al.* 2007).

Despite the importance of the above-mentioned processes, there are to our knowledge no integrated studies that have investigated the role of changing litter inputs for the soil food web and carbon processing in high-latitude bog ecosystems. In these ecosystems, springtails (Collembola) are particularly ubiquitous microarthropod decomposers and microbivores. The aims of the present study were therefore to investigate (1) the role of soil invertebrate (springtail) species composition in organic matter processing in a subarctic bryophyte dominated peatland, and (2) how vascular plant litter input in these peatlands impacted on springtail abundance, diversity and litter carbon processing contributions. By using a stable ^{13}C isotope tracer approach we investigated the relative contributions of moss vs. vascular plant leaf litter to the fine scale vertical spatial distribution and nutrition of springtail species. We have used carbon isotopes, firstly, because carbon is the key element of interest for peatland climate feedback (Gorham 1991; Dorrepaal *et al.* 2009) and, secondly, since the $\delta^{13}C$ signal of diet propagates with very

little fractionation (less than 1‰) into consumers (Deniro and Epstein 1978), which allows distinction between the food sources with different ^{13}C signatures (Fry 2006). Through addition of ^{13}C enriched vascular plant litter to an non-enriched peat system, and vice versa, we studied how springtail communities responded to changes in litter input by analyzing their diversity, abundance, diet choice ($\delta^{13}C$ signature), and species specific responses to leaf litter composition. If chemical properties of litter will dominate the response of the soil invertebrate community we hypothesize there to be shifts in diet choice of springtails, and thus in their $\delta^{13}C$ values. If microclimate is the dominant driver, we do not expect diet shifts, but rather changes in species abundances when leaf litter composition changes. We also hypothesize that individual species differ in their response to vascular plant litter input with respect to chemical versus microclimatic aspects. We will finally try to link the carbon processing properties of the (changing) springtail communities to mass loss patterns of mosses and/or vascular plant litter.

Methods

Study site

The experiment was carried out in Abisko, North Sweden (68º 21'N,18º49'E, 340-370 m above mean sea level) from June 2009 until August 2010, preceded by plant ^{13}C labeling in 2008. Precipitation in this area is low, on average 320 mm per year, and average monthly temperatures vary generally between -15°C (February) and 15°C (July) with a winter mean of -6°C and a summer mean of 7°C. The growing season lasts about 130 days (Krab *et al.* 2010). The location of the experiment was on a blanket bog on a bank of Lake Torneträsk near the Abisko Research Station. This bog is dominated by the moss *Sphagnum fuscum* (Schimp.) H. Klinggr., vascular plants have a cover of about 25%, mainly consisting of *Empetrum hermaphroditum* Hagerup, *Betula* nana L., *Vaccinium microcarpum* L., *Vaccinium uliginosum* L., *Rubus chamaemorus* L., *Eriophorum vaginatum* L., and *Calamagrostis lapponica* (Wahlenb.) Hartm. (Aerts *et al.* 2009). This bog was surrounded by forest dominated by *Betula pubescens* Ehrh.

Isotope labeling of moss and leaf litter

In the summer of 2008, litter of *Sphagnum fuscum* (Schimp.) H. Klinggr. and *Betula pubescens* Ehrh. ssp tortuosa (Ledeb.) Nyman (from here on referred to as '*Sphagnum*' and '*Betula*') was labeled by sequential pulse labeling of the living plants with ^{13}C enriched CO_2. For *Sphagnum*, green parts of vascular plants were mechanically removed from a plot of 1 m^2 preceding the labeling. $^{13}CO_2$ was added to the headspace of a transparent chamber that covered the 1 m^2 plot completely (0.2 m^3). $^{13}CO_2$ was obtained by dissolving ^{13}C labeled sodium bicarbonate (99%) in sulfuric acid (2M) to form an extra 400 ppm of $^{13}CO_2$. We conducted 13 labeling sessions, which each lasted for 12 hours. At the start of the experiment, the used living moss core of labeled *Sphagnum* contained one layer of isotopically enriched moss. This layer consisted out of last years freshly grown moss; this resulted in an enrichment located in the two top centimeter of the core (Table S1).

Five *Betula* trees (2 m height) were enriched by adding $^{13}CO_2$ to the air trapped by a closed plastic bag (2x2 m) that was placed over the canopy and wrapped airtight around the tree trunk. *Betula* trees received 5 pulse-labeling sessions that lasted 20 hours. After the final pulse-labeling session,

a net was wrapped around the tree trunk to collect the senesced leaf litter.

A minimum interval of 24 hours between all labeling sessions let the plants recover from coverage. The labeling resulted in an average ^{13}C enrichment of 23.3 ‰ for *Sphagnum* mosses and 45.7 ‰ for *Betula* leaf litter compared to their natural ^{13}C abundances (Table 1).

Table 1. Average $\delta^{13}C$ values of ^{13}C enriched and non-enriched *Sphagnum* cores (for 8 cm and 4 cm deep cores, respectively; n=2) and Betula leaf litter (n=7).

		Natural ^{13}C (‰)	Enriched ^{13}C (‰)
Sphagnum fuscum	8 cm	-27.46 ± 0.82	-4.15 ± 8.10
	4 cm		2.70 ± 1.86
Betula pubescens		-31.79 ± 0.22	13.86 ± 8.66

Experimental design

We used a semi-open mesocosm experiment, which was set up in June 2009. Transparent Perspex tubes of 20 cm depth and an inner diameter of 12 cm were inserted 8 cm deep into a micro-site in the *Sphagnum* bog. The bottoms of these tubes were closed with a fine mesh (30 μm) so that gas and water exchange was possible, but microarthropods could not escape the mesocosm. The top of the mesocosm was open to optimize gas and water exchange. As this top protruded 12 cm above the cores and the inner sides of the tubes were very slippery, the springtails could not escape. A field setting was used to retain natural moisture and pH conditions of the *Sphagnum* peat moss.

These mesocosms were filled with either (1) 20 g (fresh weight) of *Betula* litter, with leaves cut in half to optimize mixing in the mixtures, (2) a *Sphagnum* core of 8 cm depth, or (3) a combination of the two containing a *Sphagnum* core of 4 cm and 10 g of *Betula* leaf litter. The *Sphagnum* cores were placed into the mesocosm first, and *Betula* litter was added to mimic its litter input in a realistic field setting (only in the top layer of moss). The cut *Betula* leaves were inserted in the *Sphagnum* core such that the top 4 cm of the core contained a mixture of approximately 50% of each species and that the contact between the moss and the *Betula* leaf litter was optimal.

Each mesocosm contained a small litterbag (6x6 cm) with a relatively large mesh size (3 mm) to allow soil invertebrates to enter, filled with exactly the same litter type as its surrounding litter. Each litterbag contained approximately 5 g of air-dried litter; the litterbags of the mixtures were filled with 2.5 g of each litter type. Litterbags were inserted in the center of the mesocosm.

Of each single-litter species mesocosm there was a ^{13}C enriched and a natural ^{13}C abundance (non-enriched) treatment. For the litter mixtures, there were three ^{13}C treatments; one where the *Sphagnum* was isotopically enriched, one where the *Betula* litter was enriched, and one treatment where both litter species had a natural ^{13}C abundance. This resulted in a set-up with seven treatments that were replicated seven times in a Latin square design (Mead *et al.* 2003). ^{13}C enriched *Sphagnum* cores were collected from the labeled plots and natural ^{13}C abundance *Sphagnum* cores were collected randomly around the labeled plots (max distance 3 m). *Betula* leaf litter was collected either from the ^{13}C enriched trees or from non-^{13}C enriched trees in the fall of 2008.

Each mesocosm contained its original soil fauna community. To compensate for the fact that our (^{13}C enriched/non-enriched) *Betula* leaf litter did not contain any fauna, we extracted soil microarthropods from *Betula* litter in nearby birch forest, which was added at natural litter/moss densities to the *Betula* mesocosms in the experiment. Subsequently, we added soil fauna representing both peat bog and birch forest (extracted from similar *Sphagnum* cores and *Betula* litter) to make sure that all cores received the full potential species pool at the start of the experiment. At time of harvest springtail densities in the mesocosms represented realistic field densities (Krab *et al.* 2010).

Harvest

The harvest of the mesocosms was carried out in August 2010, after a total running time of 406 days. During the harvest, litterbags were carefully removed from each mesocosm after which the litter samples were cleaned and separated by hand, dried for 48 hours at 60ºC and (re-)weighed (to the nearest mg) for calculation of % mass loss.

To extract the soil fauna from the mesocosms, the *Sphagnum*/*Betula* cores were transferred to a Tullgren Funnel fauna extractor (Van Straalen and Rijninks 1982) in which the soil cores were turned upside-down, and in which the animals were extracted for 3 weeks and stored in 70% ethanol. Although ethanol is known to affect carbon isotope values by up to 0.5‰ (Krab *et al.* 2012), it was chosen as preservation medium nonetheless because the species identification required a liquid medium. In addition, we expected ^{13}C values to considerably diverge more than 1‰ within and between the treatments because of the one to two orders of magnitude larger variation in litter signature after the pulse labeling. After the extraction, litter species of each mesocosm core were cleaned and separated by hand, dried at 60ºC for 48 hours and weighed.

For each soil fauna sample, springtails were identified and counted, and from four larger and abundant springtails species, adults were selected for ^{13}C analysis: *Folsomia quadrioculata*, *Protaphorura pseudovanderdrifti*, *Ceratophysella denticulata* and *Lepidocyrtus lignorum*. As not all samples contained all species, species-specific ^{13}C analyses were conducted when possible, resulting in a maximum of 7 measurements per species per litter treatment and a minimum of 4. (Fig. 3) Springtails were identified to species level using the keys of Fjellberg (Fjellberg 1998, 2007).

Stable isotope analysis of litter and soil fauna

After milling the samples and homogenizing, approximately 1 mg dry mass of each litter species was weighed (to the nearest μg) into 4 x 3.2 mm tin capsules (Elemental Microanalysis Limited, Okehampton, UK). As the weight of separate soil fauna species ranged between 0.015-0.507 mg of dry mass, 1-25 individuals per sample were used for ^{13}C analysis. Details of isotope measurements of soil fauna were as in Krab *et al.* (2012).

Carbon isotopic composition was determined by an elemental analyzer (NC2500, ThermoQuest Italia, Rodano, Italy) coupled online to a stable isotope ratio mass spectrometer (Deltaplus; ThermoFinnigan, Bremen, Germany). For calibration, IAEA 601 (-28.81‰), USGS 40 (-26.39‰), and USGS 41 (37.63‰), were used. The reproducibility of the $\delta^{13}C$ analysis determined by repeated analysis of an internal standard (Bovine liver with 50% C and $\delta^{13}C$ =

-17.60), was within 0.2‰ (n=3). Carbon isotopic abundance is reported in δ-notation relative to the Vienna PeeDee Belemnite standard as:

$$\delta^{13}C\ (‰) = \frac{(^{13}C/^{12}C)_{sample} - (^{13}C/^{12}C)_{standard}}{(^{13}C/^{12}C)_{standard}} * 1000$$

Calculations and Statistics

Differences in total springtail density among mono-specific and mixed litter types were tested by one-way ANOVA. Expected total density of springtails in a mixed litter combination was calculated using springtail abundance and volumes of the mono-specific treatments and their proportions in a mixture. A correction was made for expected springtail density in 4 cm deep *Sphagnum* cores in the litter mixture treatments, since 70% of their abundance is found in the top 4 cm of an 8 cm core (Krab *et al.* 2010).

To check for similarity between springtail communities of the different litter treatments, we calculated the Bray-Curtis similarity index, which varies between 0, for completely dissimilar communities, and 1, for completely similar communities. (Bray and Curtis 1957) as:

$$1 - BC = 1 - \frac{\sum |n_{1i} - n_{2i}|}{\sum (n_{1i} + n_{2i})}$$

Where n_{1i} is the number of individuals of the ith species in community 1 and n_{2i} is the number of individuals of the ith species in community 2.

To calculate ^{13}C values of our litter mixtures we used a two-source mixing model with weighted averages, which allows realistic tracking of the amounts and masses in mixtures that start with sources and calculate forwards to predicted δ values (Fry 2006). The model

$$\delta_{MIX} = \frac{m_1 * W_1 * \delta_{SOURCE1} + m_2 * W_2 * \delta_{SOURCE2}}{m_1 * W_1 + m_2 * W_2}$$

calculates the δ-value of our mixture (δ_{MIX}) by using the two average $\delta^{13}C$ values of the mono-specific mesocosms ($\delta_{SOURCE1}$ and $\delta_{SOURCE2}$), the dry masses of the litters in each mixture (m_1 and m_2) and the fractions of carbon in the two sources (W_1 and W_2). Mono-specific $\delta^{13}C$ values were averages of seven random subsamples taken from the collected (and mixed in *Betula*) mono-species litters. The calculations of the $\delta^{13}C$ values of the litter mixture were made for each replicate individually, by using the dry weights of the litters in each mesocosm, using average values for $\delta_{SOURCE1}$ and $\delta_{SOURCE2}$.

By one-way ANOVA we assessed if litters had a significantly different $\delta^{13}C$ signature, using total treatment (litter and enrichment treatment) as a fixed factor. A three-way ANOVA with factors ^{13}C enrichment, litter treatment and springtail species tested for effects of enrichment on $\delta^{13}C$ signatures of springtails. In this ANOVA analysis four springtail species were assessed, however,

not all species were present in all treatments.

To assess if $\delta^{13}C$ values of individual springtail species were significantly different within a litter and ^{13}C enrichment treatment paired t-tests (paired according to block) were used when only two springtail species (of which we had measured $\delta^{13}C$ values) were present in a litter treatment. When more than two species were present in a treatment, we carried out two-way ANOVA's, with species as a fixed factor and block (replication) as a random factor. Using one larger, more powerful test for these comparisons would have lead to un-interpretable results since differences in species' $\delta^{13}C$ values would have been lost because of the large variation in $\delta^{13}C$ values of our total litter treatments. In our statistical analyses comparing non-^{13}C enriched to enriched treatments, the normality and homogeneity of variance assumption could not always be met, due to the large variation in $\delta^{13}C$ values in the enriched treatment. However, we still carried on with the analyses since most tests showed strong effects of our treatments and ANOVA's are known to be robust to deviations from normality and homogeneity as long as the sample sizes are nearly equal (Zar 1999). Springtail and litter $\delta^{13}C$ values were not transformed as no regular transformation improved variance distributions.

The contribution of each of the two litter species to a springtail's diet in mixtures (all combinations) was calculated by using a two-source mixing model (Fry 2006). Incorporating the ^{13}C fractionation observed in the mono-specific treatments in this model was not possible because, due to the spatial patterning of ^{13}C enrichment in *Sphagnum*, estimates of ^{13}C fractionation could not be made. By using the litter signatures as end-members (Fry 2006), we assumed there to be no difference in ^{13}C fractionation over trophic levels between carbon isotopes from *Sphagnum* or *Betula*. The contribution of *Sphagnum* and *Betula* carbon to a springtail's diet was calculated using the following equation:

$$\text{SOURCE 1 (\%)} = \frac{\delta_{MIX} - \delta_{SOURCE2}}{\delta_{SOURCE1} - \delta_{SOURCE2}} * 100$$

where SOURCE 1 is the contribution of *Betula*-carbon to a species diet, δ_{MIX} is the $\delta^{13}C$ signature of the springtail, $\delta_{SOURCE1}$ is the average ^{13}C value of *Betula* litter and $\delta_{SOURCE2}$ is the average ^{13}C value of *Sphagnum*.

Differences in total dry mass loss between litters (and mixtures) were tested using a one-way ANOVA. Expected dry mass losses in a mixture were calculated using dry mass loss percentages in the mono-specific litter treatments and the proportions of the litters in a mixture. Expected dry mass loss values were calculated block-wise. Differences between observed and expected litter mass losses in the mixtures were tested using paired t-tests (since expected mass losses were calculated per block). Mass loss data met the assumptions of normality and homogeneity of variance. All statistical analyses were carried out using SPSS version 19.0 (SPSS Inc., Chicago, Illinois,USA).

Results

Springtail density

There were large differences in springtail density among litter treatments. *Betula* litter showed an average density of 495 ± 252 ind. dm^{-3} whereas *Sphagnum* cores contained 1028 ± 508 ind. dm^{-3} and litter mixtures 1424 ± 579 ind. dm^{-3} ($F_{3,66}$= 10.0, $P < 0.001$) (Fig. 1, Table S1). Densities were significantly lower in *Betula* cores than in any other litter treatments ($P < 0.05$) but did not differ between *Sphagnum* cores and the litter mixtures.

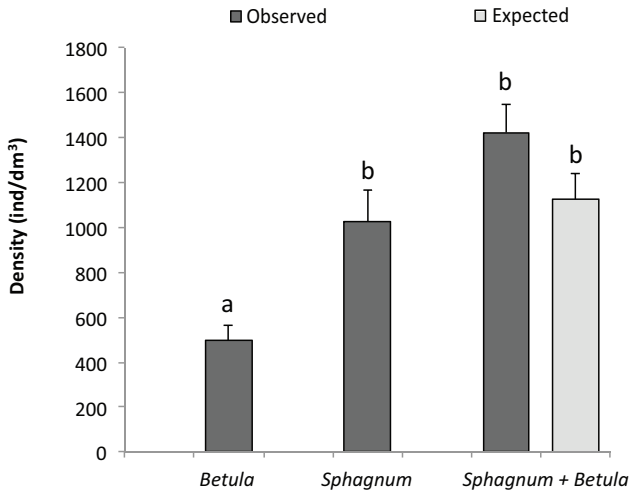

Figure 1. Springtail density (ind. dm^{-3}) in *B. pubescens* (*Betula*) litter, *S. fuscum* (*Sphagnum*) litter and in the *Sphagnum* + *Betula* litter mixture. Dark grey bars represent observed density; the light grey bar represents the expected total density (for calculation see methods). Bars that share the same letter do not differ significantly ($P > 0.05$). Data are means + SE (n=7).

Springtail diversity

Springtail species numbers were higher in *Sphagnum* cores (15 species) than in *Betula* cores (11 species), but species numbers were highest (18 species) in the litter mixture (Table S1). *Sphagnum* cores were dominated by the springtail *F. quadrioculata* (84% of total springtail density) whereas the *Betula* communities were dominated by *L. lignorum* (90% of total springtail density); the litter mixture treatments were also dominated by *F. quadrioculata*, albeit less strongly (70%) (Fig. 2). Bray-Curtis similarity was very low between *Betula* communities and *Sphagnum* and litter mixture communities (0.092 and 0.025, respectively), but high between the *Sphagnum* communities and the litter mixture communities (0.837), indicating that *Sphagnum* springtail communities changed only slightly with the addition of *Betula* litter and its compatible soil fauna. The relatively low observed dissimilarity between the *Sphagnum* community and the litter mixture treatment was only caused by the introduction of *L. lignorum* and the increased abundance of *F. truncata* and *C. denticulata* in the litter mixture springtail community (Fig. 2), however in general species diversity patterns were similar. Also the density of 'other' species increased in mixture, particularly *Isotoma viridis* (Table S1).

Carbon isotope signatures

Carbon isotope signatures of the litters between the ^{13}C non-enrichment and enrichment treatments differed strongly. ^{13}C enrichment in *Sphagnum* was 23.3‰ and in *Betula* 45.7‰ compared to their natural abundances. ($F_{7,43}$= 911, $P < 0.001$). In both *Betula* as *Sphagnum*, ^{13}C isotope signatures of springtail species in ^{13}C enriched litter treatment differed from springtails ^{13}C signatures in the non-enriched litter treatments ($F_{1,122}$= 24.8, $P < 0.001$) (Fig. 3). ^{13}C isotope values of springtails in the mono-specific treatments generally followed that of the litter, but still differed by several ‰. In both enriched and non-enriched *Betula* litter, springtails had higher $\delta^{13}C$ values than that of the plant litter, 11.8‰ and 4.5 ‰ respectively. In the ^{13}C enriched *Sphagnum* cores springtails were depleted in ^{13}C compared to the litter (16.6‰ less enriched) (Fig. 3).

The springtails *L. lignorum* and *C. denticulata* did not differ from each other in $\delta^{13}C$ signature in the *Betula* treatment, whether or not enriched (Table S2). In contrast, *F. quadrioculata* and *P. pseudovanderdrifti* differed significantly in $\delta^{13}C$ signature in *Sphagnum* in both the non-enriched ($P < 0.05$) and the enriched treatments ($F_{2,11}$ = 7.01, $P < 0.05$)(Table S2). Both *F. quadrioculata* and *P. pseudovanderdrifti* were ^{13}C enriched compared to their signatures in the non-enriched *Sphagnum* core, where they differed slightly (but significantly) in their $\delta^{13}C$ signatures (-27.3‰ vs -26.1‰). *Folsomia quadrioculata* was significantly more ^{13}C enriched in the enriched treatment than *P. pseudovanderdrifti* (-18.8‰ vs -22.9‰). *Ceratophysella denticulata* was in the non-enriched litter mixture less ^{13}C depleted than the other species ($F_{3,16}$ = 10.4, $P < 0.05$). However, the enriched *Sphagnum-Betula* mixture treatments showed no significant species effect (Table S2).

Carbon incorporation in litter mixture treatments

In all the litter mixture treatments all four main springtail species incorporated carbon from both *Sphagnum* and *Betula* litter. The two-source mixing model showed that approximately 67% of the ingested carbon in a litter mixture treatment was from *Betula.* (Fig. 4). There was no significant difference between springtail species in $\delta^{13}C$ signatures ($F_{3,42}$ = 0.506, P = 0. 681) which indicates that in a litter mixture these species do not differ in their diet.

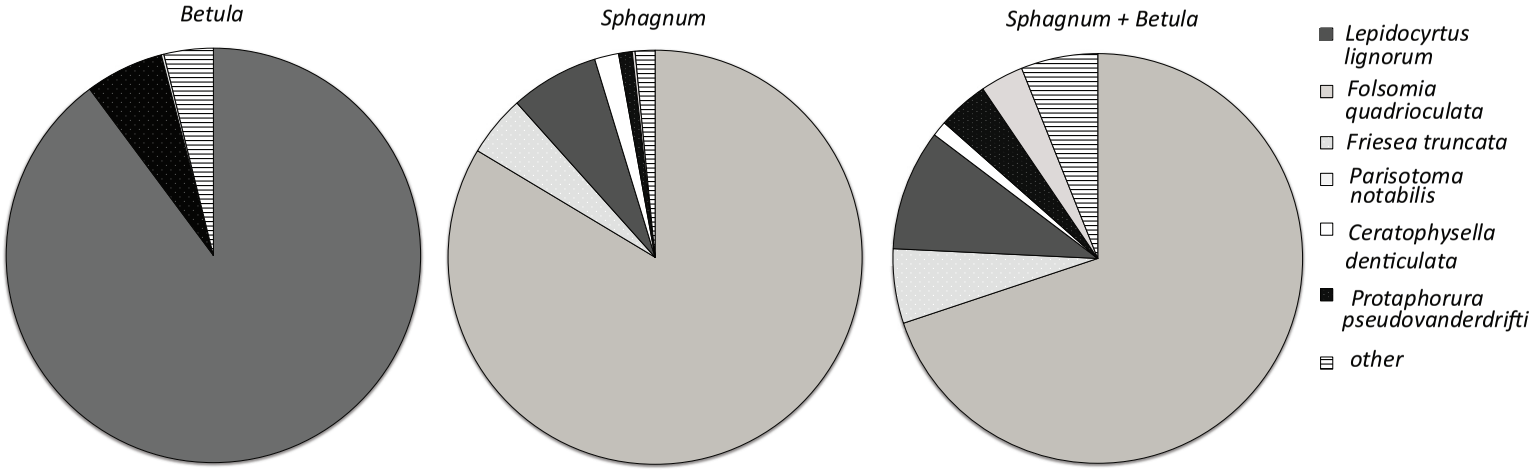

Figure 2. Springtail species distribution in *B. pubescens* (*Betula*) litter, *S. fuscum* (*Sphagnum*) and its combination. Pie parts represent densities of the springtail species (different shades of grey) relative to the total density of the springtail community. Distribution of the most abundant springtails; *Folsomia quadrioculata*, *Parisotoma notabilis*, *Friesea truncata, Protaphorura pseudovanderdrifti*, *Ceratophysella denticulata* and *Lepidocyrtus lignorum*. See Supplementary material Table S1 for full species list. Data are means (n=7).

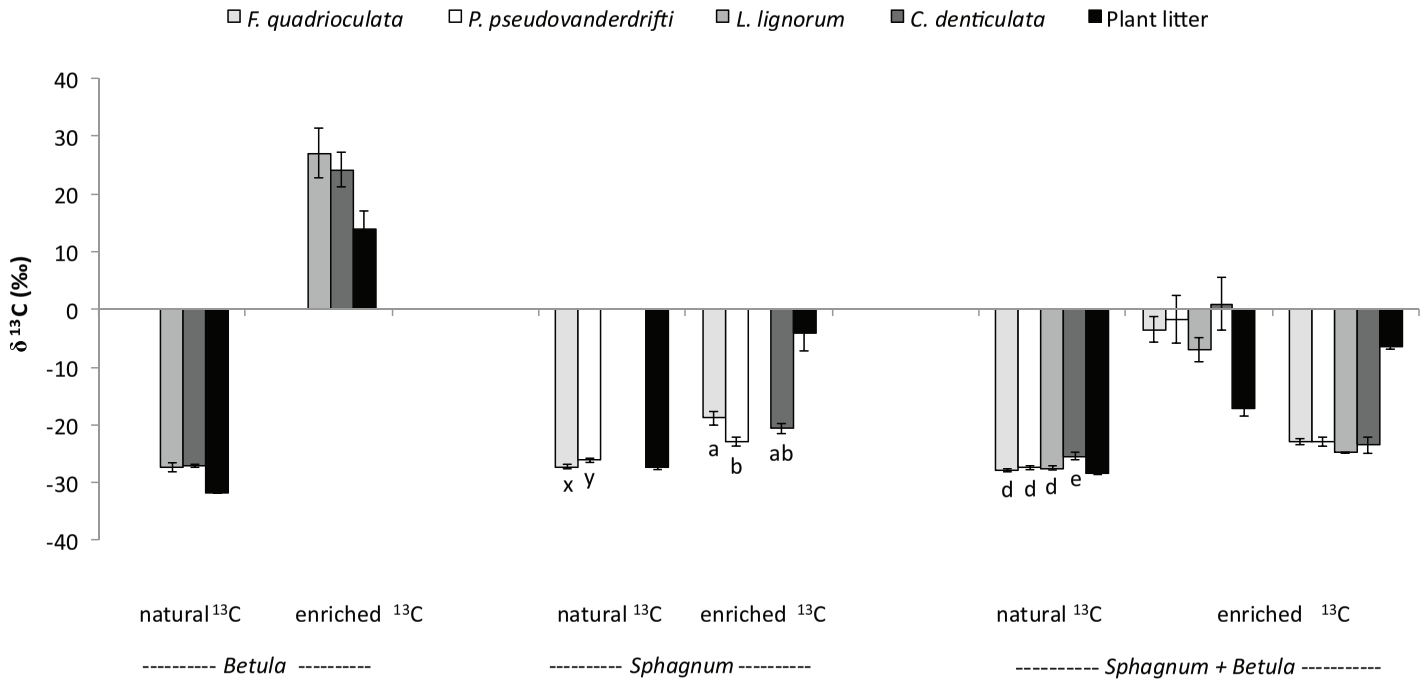

Figure 3. $\delta^{13}C$ signatures (‰) of plant litter (black bar) and four springtail species; *Folsomia quadrioculata*, *Protaphorura pseudovanderdrifti, Ceratophysella denticulata* and *Lepidocyrtus lignorum* (shades of grey). Litter treatments are *B. pubescens* (*Betula*), *S. fuscum* (*Sphagnum*) and a *Sphagnum* + *Betula* mixture. Each litter treatment is either isotopically ^{13}C enriched or non-enriched. In the ^{13}C enriched litter combination treatments either only Betula leaf litter is enriched or only Sphagnum litter. Bars without letters or that share the same letter are not significantly different from each other ($P > 0.05$). Litter ^{13}C signatures were not included in the statistical analysis. Data are means + SE (n=4-7).

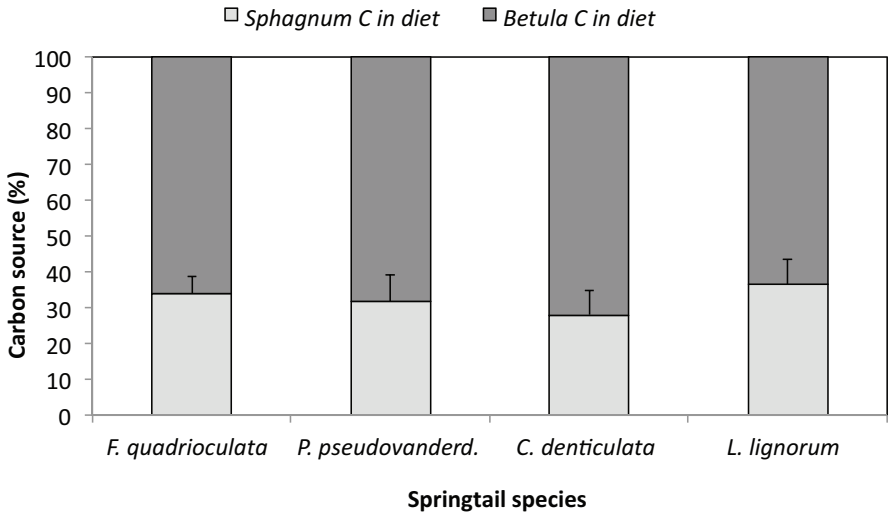

Figure 4. Incorporation of carbon from each of the two dietary litter species; *S. fuscum* (*Sphagnum*) and *B. pubescens* (*Betula*), in the mixed litter treatment based on the enriched litter treatments for four Collembola species *Folsomia quadrioculata*, *Protaphorura pseudovanderdrifti*, *Ceratophysella denticulata* and *Lepidocyrtus lignorum*. Data are means + SE (n=4-7).

Litter mass loss

Total dry mass loss differed between the litter treatments ($F_{3,66} = 46.7$, $P < 0.001$) (Fig. 5). *Betula* leaf litter lost three times as much mass as *Sphagnum* litter ($P < 0.001$). The observed total litter mass loss of a mixture was significantly larger ($P < 0.01$) than expected from mass loss of single litter species. Total mass loss in the litter mixture did not significantly differ from that of *Betula* litter. Litter mass loss of *Betula* and *Sphagnum* decomposing on their own were 16.1 ± 3.0% and 4.7 ± 2.7%, respectively, whereas mass loss of these species in mixture were 26.2 ± 4.4% and 1.9 ± 2.4%, respectively (Fig. 5). The mass loss of *Betula* litter was significantly larger in the litter combination than expected ($F_{1,33} = 58.9$, $P < 0.001$), while litter mass loss of *Sphagnum* in a litter mixture was lower than expected ($F_{1,33} = 7.61$, $P < 0.01$). The contribution of *Betula* litter to the total mass loss in a litter mixture, therefore, was significantly larger than that of *Sphagnum* litter and larger than expected from their decomposition rates in the mono-specific treatments.

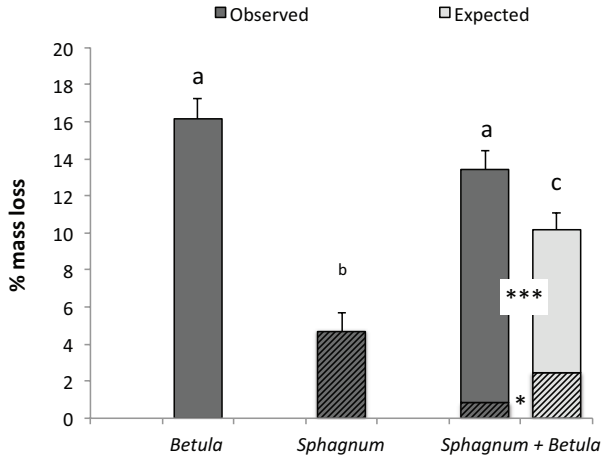

Figure 5. Total mass loss percentages of *B. pubescens* (*Betula*) and *S. fuscum* (*Sphagnum*) and the *Sphagnum* +*Betula* mixture. Dark grey bars represent observed litter mass loss (% initial dry weight); the light grey bar represents the expected total litter mass loss based on the observed litter mass loss of the individual species. Shaded bars represent the contribution of mass loss of *Sphagnum* litter to the total mass loss. The ratio between non-shaded and shaded surface area of a bar in the litter mixture treatment represents the contribution of *Betula* and *Sphagnum* litter to the total mass loss. Bars that share the same letter are not significantly different from each other. For the differences in individual mass loss percentages of *Betula* and *Sphagnum* litter in the observed and expected litter mixture bars, * : $P < 0.05$; *** $P < 0.001$., Data are means + SE (n=7).

Discussion

Using the transfer of ^{13}C labeled litter into the springtails we showed that springtails do not only contribute to the decomposition of peat moss, but by feeding on different carbon sources, they also differ in their role in this key soil process. When vascular plant litter enters these ecosystems, however, their role in organic matter processing changes and species-specific differences in diet choice disappear. When *Betula* litter enters a *Sphagnum* peat bog system it becomes the main carbon source of the springtails diet regardless of the identity of the springtail species. This suggests that the relatively high nutritional quality of *Betula* litter compared to that of *Sphagnum* (Dorrepaal *et al.* 2005) overrules species-specific differences in diet choice of peat moss inhabiting springtails. This supports the hypothesis that changing the chemical quality of the diet is the main way in which vascular litter inputs alter the relative contribution of high-latitude springtails to breakdown of mosses versus vascular plant litter, and consequently in carbon turnover.

Furthermore, the observed springtail diet shifts correspond to mass loss patterns of the litter mixture of *Sphagnum* and *Betula*, suggesting that these diet shifts have consequences for decomposition rates of the two litter species. However, before we can draw firm ecological conclusions from these findings, we need to address the main ifs and buts of the details of our experimental setup and results.

$\delta^{13}C$ values of litter and springtails

Although the $\delta^{13}C$ values of springtails in the mono-specific treatments generally followed that of the litter they lived in, there were still some unexpected differences. Springtail isotopic signatures in *Betula* showed $\delta^{13}C$ values several ‰ above the $\delta^{13}C$ values of their litter, whereas animal tissues are expected to be enriched by only 0.4‰ compared to their diet (Post 2002). Since springtails are considered to be mostly fungal feeders (Lussenhop 1992) this would theoretically lead to a maximum ^{13}C enrichment of 0.8‰, which is still less than we observed (11.8‰). Litter ^{13}C enrichment using elevated CO_2 can affect the decomposability of leaf litter. In addition, microorganisms are known to select for the enriched carbon pools (Cotrufo *et al.* 2005). Since the variation in $\delta^{13}C$ signatures of enriched *Betula* litter was rather large, ($\delta^{13}C$ values ranged between 5.1-22.5‰) fungi could have been more enriched than the *Betula* litter.

^{13}C signatures of springtails in enriched *Sphagnum* cores were lower than expected, firstly, because springtails had been present in the *Sphagnum* core before the enrichment treatment started. Secondly, the source of enrichment was only present in the top 2 cm of the moss core. *Sphagnum* cores were enriched during one growing season and thus formed an enriched 'fresh' litter layer on the surface instead of a homogeneously enriched substrate from top to bottom.

Functional differences between springtails in Sphagnum

While soil invertebrates can affect carbon cycling by physically changing their environment, most of their involvement is caused by their feeding activities (Lavelle 1997). Diet choice and feeding rates determine their impact on carbon cycling and consequently their functional role. ^{13}C-values can be used as a proxy for diet choice (Scheu and Folger 2004) and we, therefore, consider differences in these values to correspond to differences in function.

Springtail species in *Betula* litter did not differ in their ^{13}C values. However, we did find relatively small but significant differences between two abundant (high biomass) springtail species in *Sphagnum*. *Folsomia quadrioculata*, and *P. pseudovanderdrifti* differed in ^{13}C values both in the non-enriched and the enriched treatments. Although both springtail species were significantly enriched in the ^{13}C enriched *Sphagnum* cores, suggesting diet overlap, *F. quadrioculata*, showed higher ^{13}C values than *P. pseudovanderdrifti*. This indicates that their tissue contained more carbon from the isotopically enriched fresh litter layer than the deeper living *P. pseudovanderdrifti* (Krab *et al.* 2010). In the non-enriched treatments the patterns were opposite, i.e. *F. quadrioculata* was more depleted in ^{13}C than *P. pseudovanderdrifti*. This difference can also be explained by the vertical stratification patterns of these species, since older, more decomposed litter is generally less ^{13}C-depleted than 'fresh' litter higher up in the peat profile (Balesdent *et al.* 1993; Hishi *et al.* 2007; Dorrepaal *et al.* 2009). However, we cannot exclude that these subtle differences in $\delta^{13}C$ signature could be due to a preservation effect (Krab *et al.* 2012).

Vascular litter input changes springtail diets

The addition of *Betula* litter to a *Sphagnum* core did not change the springtail density but its diversity increased by incorporating more springtail species into the system. Since *F. quadrioculata* remained by far the most dominant species, the similarity between a *Sphagnum* springtail

community and that of a *Betula-Sphagnum* litter combination was high, suggesting that springtail species composition, at least in a horizontal space, is not very sensitive to vascular litter input. This can be explained by the change in diet choice of the *Sphagnum* soil invertebrate community. After addition of *Betula* litter, almost 70% of the carbon ingested by *F. quadrioculata* and *P. pseudovanderdrifti*, the two characteristic *Sphagnum* inhabiting species, was coming from *Betula*. Springtails characteristic for the *Betula* community, i.e. *L. lignorum* and *C. denticulata*, showed a similar response pattern as their tissues contained 30% of *Sphagnum* carbon in a moss/litter combination. This shift in diet choice can be explained by the higher resource quality of *Betula* litter compared to *Sphagnum* for decomposers (Lang *et al.* 2009). Surprisingly, the previously observed functional difference between *F. quadrioculata* and *P. pseudovanderdrifti* disappeared completely. Moreover, different springtail species showed a common response to the combined *Sphagnum* and *Betula* litter substrate availability.

Springtails are known to use fungi as their main food source but are also considered to be opportunistic feeders (Petersen and Luxton 1982; Lartey *et al.* 1989; Lussenhop 1992). The contribution of *Sphagnum* and *Betula* to a springtail's diet could have changed: (1) because of a change in a springtail's litter diet, (2) by changes in the resource quality of the fungal community and/or (3) by selective feeding on fungal species that specifically break down *Sphagnum*, *Betula* or a combination of both (Varga *et al.* 2002; Schneider and Maraun 2005). Springtail δ^{13}Cisotope values might, therefore, be a reflection of the isotope value of the microbial community or of specific fungal species acquired by selective grazing (or both). Since we assigned the functional differences between *F. quadrioculata* and *P. pseudovanderdrifti* to their vertical distribution pattern, these results suggests that either litter inputs overrule these patterns, i.e. deeper living species move to the top layer to feed on the more nutritious food source, or, that fungal hyphae grow throughout the whole core and thereby change the carbon diet of deeper living species. Both possible interpretations of our results are consistent with the hypothesis that changing the chemical quality of the diet is the main way in which vascular litter influx affects carbon turnover by springtails in peat bogs.

Ecological implications

As climate change is expected to increase the occurrence of shrubs and thus vascular plant litter influx in peat-dominated ecosystems, this might have consequences for decomposition patterns of both their litters. Mass loss of *Sphagnum* and *Betula* litter and its combination showed a pattern consistent with that of the carbon source patterning in springtails. Mass loss of *Betula* litter was higher when decomposing in combination with *Sphagnum* than by itself and *Sphagnum* decomposed slower in combination with *Betula* litter. This pattern has previously been observed in a study by Wardle *et al.* (2003) where decomposition of vascular plant litters was promoted by the presence of feather mosses, and moss decomposition was inhibited in mixture. Based on our findings, we propose that these decomposition rates are caused by stimulation of the moss decomposer community due to chemical properties of the litter rather than by increased moisture conditions due to the water holding capacity of the mosses (Wardle *et al.* 2003; Hayward *et al.* 2004) or increased habitat complexity (Hansen 2000; Bardgett and Wardle 2010).

Our results show that, at least in earlier stages of shrub encroachment, springtail species composition is hardly affected by its litter input. Although soil invertebrates are known to show

niche partitioning (Erdmann *et al.* 2007; Schneider *et al.* 2005) and selective feeding behavior (Varga *et al.* 2002), they seem to be very plastic in their diet choice, and easily switch from one food source to another (Endlweber *et al.* 2009). Therefore we do not expect large shifts in species composition due to the increasead resource quality caused by vascular plant litter input. Decomposition patterns however, will significantly change, since soil invertebrates show a strong preference for a diet containing carbon from vascular plant litter above that of mosses.

On the longer term, however, when shrub coverage increases further at the cost of peat moss, we expect that soil invertebrate communities will change towards those found in *Betula* dominated ecosystems, because of strong changes in microclimatic conditions, the increased presence of roots, and the decrease of occurrence of peat moss and its specific microclimatic conditions hosting the soil invertebrate community. This will consequently lead to a lower springtail density and decreased decomposition rates of *Betula* relative to that of the situation in which moss and vascular plant litter were mixed.

This study is one of the very first to show empirically that in case of vegetation shifts, the plasticity of the decomposer community in respect to diet composition might be even more important than its interspecific differences, regarding its effects on organic matter processing. Changes in litter decomposition patterns and rates caused by vegetation shifts might well be due to plasticity and stimulation of the present decomposer community even without any major changes in its species composition. On the longer term, when the relative dominance of vascular plants increases further, interspecific differences in sensitivity to microclimatic conditions and consequential competition effects might get more important in structuring soil invertebrate communities and their role in organic matter processing. These observations might contribute considerably to the current debate about the importance of (phenotypic) plasticity versus interspecific functional differences (Miner *et al.* 2005; Berg and Ellers 2010)

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Supporting Information

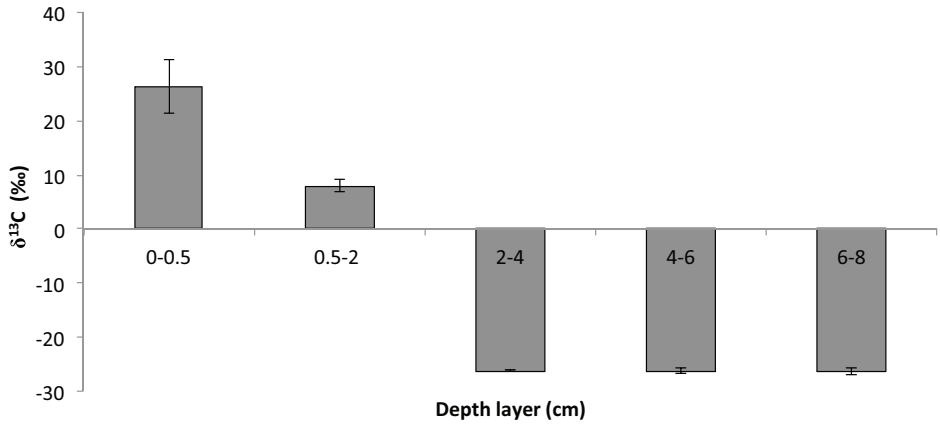

Figure S1. $\delta^{13}C$ signatures (‰) of *Sphagnum fuscum* litter at various depths (0-0.5, 0.5-2, 2-4, 4-6 and 6-8 cm) in the peat profile. Means of 2 replicates, error bars are standard errors.

Table S1. Springtail species list and densities of communities in *Sphagnum* cores, *Betula* litter and its combination.

Species	*Betula*	*Sphagnum*	Litter combination
Folsomia quadrioculata	1 ± 2	861 ± 500	995 ± 483
Friesea truncata	0 ± 0	71 ± 37	136 ± 76
Parisotoma notabilis	0 ± 0	49 ± 35	84 ± 56
Ceratophysella denticulata	30 ± 12	11 ± 11	57 ± 70
Lepidocyrtus lignorum	445 ± 251	2 ± 3	49 ± 24
Isotoma viridis	0 ± 1	0 ± 1	40 ± 146
Desoria sp.	4 ± 7	8 ± 10	23 ± 38
Protaphorura pseudovanderdrifti	0 ± 0	19 ± 21	17 ± 15
Micranurida pygmea	0 ± 0	4 ± 5	9 ± 21
Isotomiella minor	0 ± 0	0 ± 0	5 ± 15
Anurida sp.	0 ± 1	2 ± 2	4 ± 7
Entomobrya nivalis	10 ± 10	0 ± 1	3 ± 5
Sminturinus elegans	2 ± 2	1 ± 1	1 ± 2
Dicyrtoma fusca	1 ± 1	0 ± 0	1 ± 1
Arrhopalites principales	0 ± 0	0 ± 1	0 ± 1
Neanura muscorum	0 ± 0	1 ± 1	0 ± 1
Dicyrtomina minuta	0 ± 0	0 ± 0	0 ± 0
Entomobrya marginata	2 ± 9	0 ± 0	0 ± 0
Unknown	0 ± 1	0 ± 0	1 ± 2
Total	495 ± 252	1028 ± 508	1424 ± 579

Table S2. Statistical analyses for within treatment springtail species differences in $\delta^{13}C$ signatures.

Litter	Enrichment	Collembola species identity			Blocking		
		d.f.	*F*	*P*	d.f.	*F*	*P*
Betula							
	non-enriched[a]	6		0.839			
	enriched[a]	6		0.591			
Sphagnum							
	non-enriched[a]	6		< 0.05			
	enriched[b]	2	7.014	< 0.05	6	2.693	0.074
Litter combination[b]							
	non-enriched	3	10.44	< 0.001	6	4.066	< 0.05
	Betula enriched	3	2.441	0.168	6	1.416	0.253
	Sphagnum enriched	3	1.357	0.296	6	0.471	0.819